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The Southern Ocean Benthic Fauna and Climate Change: A Historical Perspective [and Discussion]

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The Southern Ocean benthic fauna and climate change: a historical perspective

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SUMMARY

Environmental change is the norm and it is likely that, particularly on the geological timescale, the temperature régime experienced by marine organisms has never been stable. These temperature changes vary in timescale from daily, through seasonal variations, to long-term environmental change over tens of millions of years. Whereas physiological work can give information on how individual organisms may react phenotypically to short-term change, the way benthic communities react to long-term change can only be studied from the fossil record. The present benthic marine fauna of the Southern Ocean is rich and diverse, consisting of a mixture of taxa with differing evolutionary histories and biogeographical affinities, suggesting that at no time in the Cenozoic did continental ice sheets extend sufficiently to eradicate all shallow-water faunas around Antarctica at the same time. Nevertheless, certain features do suggest the operation of vicariant processes, and climatic cycles affecting distributional ranges and ice-sheet extension may both have enhanced speciation processes. The overall cooling of southern high-latitude seas since the mid-Eocene has been neither smooth nor steady. Intermittent periods of global warming and the influence of Milankovitch cyclicity is likely to have led to regular pulses of migration in and out of Antarctica. The resultant diversity pump may explain in part the high species richness of some marine taxa in the Southern Ocean. It is difficult to suggest how the existing fauna will react to present global warming. Although it is certain the fauna will change, as all faunas have done throughout evolutionary time, we cannot predict with confidence how it will do so.

1. INTRODUCTION

The present public and scientific concern with global environmental change has stimulated much interest in how an increase in mean global temperature might affect living organisms. There are several ways in which we can examine this problem experimentally, including detailed physiological studies of the temperature responses of organisms, and manipulation of small enclosed communities. However, although widespread interest in environmental variation is a recent phenomenon, global change itself is not. It is likely that the temperature régime experienced by organisms has, at least on the geological timescale, never been stable. Moreover, the temporal scales over which this variation occurs are very varied and marine organisms are subject to change in temperature on timescales varying from daily to evolutionary.

Whereas the fossil record can tell us little of the effects of short-term environmental variation, it can provide a powerful tool for investigating the response of faunas to long-term climate change. In this paper we have therefore chosen to look at how marine invertebrates have responded in the past to climate change, concentrating in particular on the shallow-water benthic fauna of the Southern Ocean.

2. THE MODERN FAUNA

In contrast to the paucity of life in the Antarctic terrestrial environment, the Southern Ocean shallow-water marine fauna is abundant and diverse. In soft substrata the species richness is fully comparable with more temperate regions (Richardson 1976) and the infaunal biomass and density are as great as anywhere else in the world (Lowry 1975; Dayton & Oliver 1977; Richardson & Hedgpeth 1977; Arnaud *et al.* 1986; Jazdzewski *et al.* 1986; Voß 1988). Hard substrata below the level of ice-scour are characterized by dense communities dominated by suspension feeders. Biomass can be high (White & Robins 1972) but many of these sessile organisms are from groups that are only poorly studied in the Southern Ocean and we know little of the taxonomy or species richness of this fauna.

Several groups, however, are strikingly low in species diversity in the Southern Ocean, notably decapods, bivalve and gastropod molluscs, and teleost fish. Although it is tempting to ascribe a single cause to these common patterns, detailed examination reveals important differences between the various taxa. Thus the fish fauna is dominated by a single group, the Notetheniiformes, which appears to have undergone a classical adaptive radiation (Eastman &

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Grande 1989); the bivalve fauna is striking in the paucity of many traditional epifaunal and infaunal forms, and the gastropod fauna, although low in species overall, contains several groups that appear to be in the process of speciating rapidly (Clarke & Crame 1989; Crame 1992).

The low species richness at high latitudes of molluscan groups has been instrumental in establishing the concept of a latitudinal cline in diversity (Sanders 1968; Stehli *et al.* 1967, 1969). This result is frequently extended to other taxa and an assumption made that all groups are species poor at high latitudes. For some taxa this may not be the case, and several groups have been described as notably rich in species in the Southern Ocean, including sponges, bryozoans, polychaetes, amphipods and isopods (see Clarke & Crame (1989) for original references). The situation is more complex than previously realized and we cannot assume that a simple latitude–diversity model is appropriate for the shallow water fauna as a whole (Clarke 1992).

One interesting global biogeographic pattern shown by marine molluscs, and several terrestrial taxa, is that the latitudinal ranges of polar species are wider than those of tropical species; this has been termed *Rapoport's Rule* (Stevens 1989). The explanation for this pattern is far from clear but if it reflects a more restricted niche width in tropical species, it may be related to the apparent ability of the tropics to support a greater number of species per unit area than elsewhere.

3. THE ORIGIN OF THE MODERN FAUNA

(*a*) *Evolutionary history of the Antarctic benthos*

The origin of the Southern Ocean marine fauna has long intrigued biologists, and suggestions have included colonization of the continental shelves from the deep sea, colonization from South America along the Scotia arc, and evolution *in situ*. In the opinion of many observers, living polar biotas are the product of an increasing physical isolation of continents and oceans through eons of time. This is particularly so in the south polar regions where, over the last 150 Ma, the Antarctic continent has become progressively separated from the other austral landmasses. Much of what we see today in the marine realm is held to be a classic product of evolution in isolation (Lipps & Hickman 1982), but, as with all living marine communities, the Southern Ocean marine fauna comprises a mixture of taxa with different histories. Some taxa have been present for a long time, some are newly arrived; some groups may be speciating rapidly, others perhaps in the process of becoming extinct.

Nevertheless, there is one aspect of the Southern Ocean that makes the question of the origin or age of the modern fauna a legitimate one. The continental shelves around Antarctica show extensive evidence of having been covered by ice during previous glacial maxima. It is therefore important to establish whether there has ever been a time when the continental ice of Antarctica has extended to cover all of the continental shelves, and thus wipe out the Southern Ocean shallow-water fauna completely. Although evidence from sediment structure, ice-rafted debris and continental shelf topography suggests that ice has extended over many areas of the continental shelf around Antarctica over at least the last 30 Ma (Barrett *et al.* 1989; Barron *et al.* 1991), it is not yet clear whether these extensions were simultaneous and hence whether they would have been sufficient to eradicate the biota completely (Kennett & Barker 1990).

The evidence from the Southern Ocean is equivocal. Whereas sedimentological evidence suggests repeated grounding of large ice sheets beyond the present-day shelf edge, the adaptive radiation of certain teleost fish (Eastman & Grande 1989; Gon & Heemstra 1990), isopods (Brandt 1991) and gastropods suggests a long history of evolution *in situ* (Clarke & Crame 1989). Although some taxonomically difficult (but by no means minor) groups remain to be studied, it is now generally accepted (Dell 1972; Knox & Lowry 1977) that the Southern Ocean fauna as a whole is composed of: (i) relict autochthonous taxa; (ii) organisms derived from adjacent deep ocean basins; (iii) organisms dispersing from South America along the Scotia arc; and (iv) organisms which have spread in the opposite direction from Antarctica northwards along the Scotia arc.

The high latitudes have traditionally been regarded as recipients of taxa that originated elsewhere. The major areas of diversification have usually been assumed to be the tropics, whereas the polar faunas were regarded essentially as the result of colonization from elsewhere. The high diversity of many taxa in the Southern Ocean, and palaeontological studies in Antarctica, have led to the realization that this traditional picture of faunal diversification is misleading. We now know that polar biotas are not totally isolated from those of other major regions on the Earth's surface, even at the present day. In an attempt to show the ways in which there may have been a dynamic interchange between high- and low-latitude faunas through time, Crame (1992) devised three simple evolutionary models.

In the first of these the polar regions are regarded essentially as refugia for adaptively anachronistic taxa that have been displaced progressively across meridional competition gradients. For example, the Southern Ocean includes taxa such as bryozoans and brachiopods together with relicts such as hexactinellid sponges and the bivalves *Limopsis*, *Astarte* and *Thracia* (Knox & Lowry 1977; Vermeij 1978, 1986). In the second model almost the reverse procedure is envisaged, with the polar regions exporting novel taxa to lower latitudes. Intuitively, such a scenario might seem less likely, but in the geological past much more shallow-water habitat was available in the high latitudes, and the climates there were more benign. Antarctica may have been an important centre of origin for a variety of marine invertebrate taxa (Crame (1992) and references therein; see also below).

Finally, a third model emphasizes that vicariant processes may have been just as important as dispersal in the formation of polar biotas. At certain times in

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the past, widespread and/or cosmopolitan ancestral taxa are thought to have ranged from the high northern to the high southern latitudes. These ranges were then split subsequently in the equatorial regions by a variety of tectonic, climatic and oceanographic events to form the classic bipolar pattern; a surprisingly wide variety of both fossil and living marine invertebrates has amphitropical or bipolar distributions (Crame 1993; see below). These are not the only models that could be devised; they simply demonstrate three possibilities for how global ecological and evolutionary processes may have influenced the composition of polar biotas.

(*b*) *A Mesozoic legacy*

Some elements of the living Antarctic marine fauna have been in place since at least the late Mesozoic era. The subantarctic struthiolariid gastropod *Perissodonta* is perhaps the best-known example here, having a demonstrable ancestry within the late Cretaceous Weddellian Province (Powell 1951, 1965; Zinsmeister & Camacho 1980). Although Gondwana was actively disintegrating at this time, there were still substantial shallow marine connections between Antarctica and the rest of the world. These were achieved both through West Antarctica to South America, and through East Antarctica to Australia (and possibly Indonesia). Global climates were still, on the whole, equable through the greater part of the late Cretaceous (100–65 Ma) and this may well have been the time when certain tropical and subtropical taxa were displaced into more temperate regions. It may also have been the time when the ancestors of certain living bipolar taxa achieved widespread distribution. Although these are largely thought to have had Cenozoic ancestries (and are discussed below), some groups can be traced back to the late Cretaceous (buccinid gastropods (Beu & Maxwell 1990), gadoid fish (Ho 1989)). A Gondwanan legacy may be more widespread than is generally recognized at present (Clarke & Crame 1989).

4. THE INFLUENCE OF CENOZOIC CLIMATE CHANGE

Recent advances in our knowledge of stable isotope palaeothermometry have suggested that, from a mid-Cretaceous peak (approximately 100 Ma), global marine temperatures have declined to their present-day values (Hudson & Anderson 1989). However, this decline was by no means smooth, as there were both a number of marked temperature reversals and periods of relative stability that were then punctuated by abrupt falls (figure 1). The pattern is complex, with the record being divisible into a series of major cooling and warming trends (table 1). Distinct warm periods have now been well established in both the early Paleogene (at 63–52 Ma) and early Neogene (at 23–17 Ma). Minor temperature peaks within the late Miocene may be specific to the Antarctic, but that in the early Pliocene (4.8–3.6 Ma) would again seem to have been global in nature (Webb 1990).

The foregoing major trends document temperature fluctuations on a timescale of 10^6–10^7 years. Superimposed on top of these are others on a frequency of 10^4–10^5 years which are almost certainly linked to orbital (Milankovitch) cyclicity. These are most apparent in

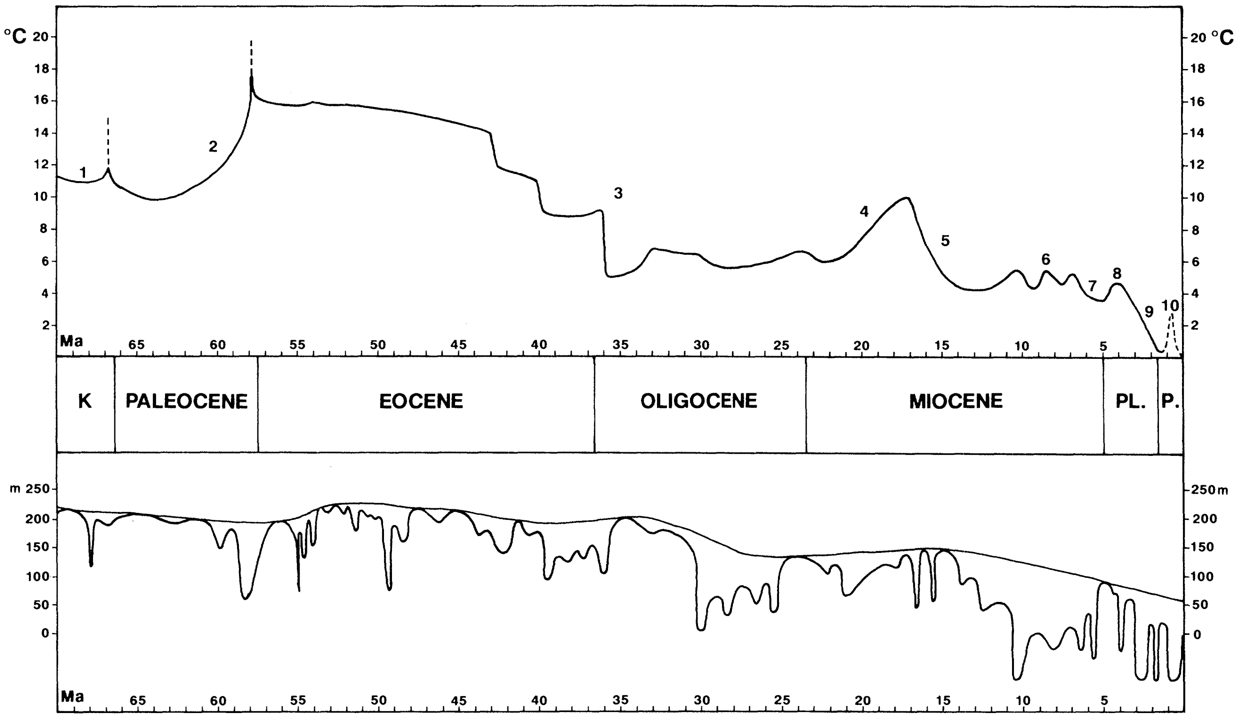

Figure 1. Temperature and sea level at high southern latitudes during the Cenozoic. The temperature curve is for surface waters, and the explanation for the values given is contained in table 1. The global sea-level curve presented in the lower half of the figure is re-drawn from Haq *et al.* (1987, figure 2).

Table 1. *Antarctic Cenozoic palaeotemperatures*

(The reference numbers identify the location of the event on the Cenozoic temperature record (figure 1).)

number	global trend	duration	notes	references
1.	cool	latest Cretaceous – early Paleocene (approximately 83–63 Ma)	Both marine and terrestrial temperature values appear to have fallen in Antarctica through the latest Cretaceous; brief excursion acoss K–T boundary but surface water values continued to fall through early Paleocene.	Stott & Kennett (1990); Stott *et al.* (1990); Francis & Frakes (1992)
2.	warm	late Paleocene – early middle Eocene (63–52 Ma)	Warming of Antarctic surface waters through the late Paleocene; remarkable temperature excursion of some 5–7°C at Paleocene–Eocene boundary, probable introduction of cool subtropical water to Antarctica; global warm phase in early–middle Eocene.	Wolfe (1985); Kennett & Barker (1990); Stott *et al.* (1990)
3.	cool	early middle Eocene – early Miocene (approximately 52–23 Ma)	Long-term cooling trend in Antarctic surface waters; cooling gradual at first but three sharp falls in late Eocene – early Oligocene led to 7–9°C reduction in surface water temperatures; despite falls, *Nothofagus* forests still present on Antarctic Peninsula; globally, warm, equable climates still widespread. Firm evidence for late Eocene glaciation in Antarctica, but size of ice cap uncertain. Major cooling event at approximately Eocene–Oligocene boundary (36 Ma), surface and bottom waters may have decreased by as much as 4°C in 75–100 ka; probable formation of first major sea ice and initiation of psychrosphere. Extent of ice cover on Antarctica through Oligocene uncertain; may have been large temperate valley glaciers rather than continuous ice sheet; pockets of *Nothogafus* vegetation still present. Circum-Antarctic current developed by late Oligocene (25 Ma).	Shackleton & Kennett (1975); Kennett (1977); Wolfe (1978); Frakes (1979); Miller *et al.* (1987); Barrett *et al.* (1989); Kennett & Barker (1990); Mohr (1990); Stott *et al.* (1990); Barron *et al.* (1991)

4.	warm	early – early middle Miocene (23–17 Ma)	Substantial increases in both surface and bottom temperatures of subantarctic waters reflects period of global warming; Neogene temperature maximum at 19.5–17 Ma.	Shackleton & Kennett (1975); Kennett (1986); Miller *et al.* (1987)
5.	cool	early middle Miocene – late Miocene (approximately 17–11 Ma)	Abrupt cooling phase from 17 to 14 Ma linked to rapid expansion of East Antarctic ice sheet and associated cooling of high latitude waters; marked increase in meridional temperature gradients.	Shackleton & Kennett (1975); Kennett (1977, 1986); Miller *et al.* (1987)
6.	intermittent cool–warm	late Miocene (approximately 11–6.2 Ma)	General cooling trend initiated in middle Miocene continues but is punctuated by brief episodes of climatic warming at 10.5 Ma, 9–8.5 Ma and 7.6–6.6 Ma.	Kennett (1986); Kennett & Barker (1990); Barron *et al.* (1991)
7.	cool	latest miocene – earliest Pliocene transition (approximately 6.2–4.8 Ma)	Moderate to severe cooling of surface waters in mid to high latitudes; development of West Antarctic ice sheet and intensification of oceanic circulation	Kennett (1977), (1986); Ciesielski *et al.* (1982)
8.	warm	early Pliocene (approximately 4.8.–3.6 Ma)	Another brief warm phase identified by both stable isotope and biogeographic studies; marine temperatures may have been 2–10°C warmer than today. Fossiliferous early Pliocene glaciomarine sediments plus reworked diatoms of same age in tillites strongly suggest there was a major deglaciation at this time; terrestrial temperatures may have been 20°C warmer than today.	Webb (1990); Hodell & Warnke (1991); Webb & Harwood (1991)
9.	cool	middle-late Pliocene (approximately 3.6–2.4 Ma)	A period of sharp climatic cooling and further ice sheet development; however, mid–late Pliocene *Nothofagus* macrofossils recorded from 85°S.	Kennett (1986); Hodell & Warnke (1991); Webb & Harwood (1991)
10.	cool	late Pliocene – Recent (2.4–0 Ma)	2.4 Ma event marks onset of bipolar glaciation.	Kennett & Barker (1990); Hodell & Warnke (1991)

the latest Cenozoic where, in the last 2.4 Ma, there may have been as many as 50 complete climatic cycles (Imbrie *et al.* 1984; Ruddiman *et al.* 1989). Such high-frequency cycles may also be detectable in the latest Miocene – earliest Pliocene, middle Miocene and, possibly, earliest Oligocene (Miller *et al.* 1987; Barron *et al.* 1991).

Although considerable progress has been made in relating nannofloral and foraminiferal distribution patterns to Cenozoic climatic change (see, for example, Ciesielski & Weaver 1974; Haq 1982; Hodell & Warnke 1991), we know far less about the responses of marine benthos particularly in the southern high latitudes where the macrofossil record is much less complete than that of microfossils. Nevertheless it is now possible to speculate meaningfully on how certain gastropod and bivalve groups may have reacted to repeated Cenozoic climatic changes.

(*a*) *Dispersal events*

Put in the simplest terms, we might expect taxa to immigrate into Antarctica during a global warming phase and emigrate from it during a cooling one. Volutid gastropods provide a possible example of the former process, for this overwhelmingly warm temperate–tropical group is represented at the present day in the subantarctic by species of *Guivillea* and *Provocator* (Powell 1965; Dell 1990). No fossil record is available for these taxa, but it would not be unreasonable to assume that they penetrated the southern high latitudes during a Cenozoic period of global warming.

The same may also be true for the pandoracean bivalve genus *Laternula*, which is represented in Antarctica today by one particularly common species, *L. elliptica* (Dell 1990). In total, some nine species of *Laternula* are known, with the centre of distribution being the Indo-West Pacific marine faunal province (Morton 1973; S. Morris, personal communication). However the fossil record of *Laternula* is, at best, equivocal, with authenticated Pliocene species being known from both Antarctica and Pakistan (Soot-Ryen 1952; Pickard *et al.* 1988; N. J. Morris, personal communication). Probable Eocene representatives of the genus have recently been described from Patagonia (Griffin 1991), but the connections with late Cretaceous stem taxa are not yet fully known. It is not impossible that *Laternula* colonized the Indo-West Pacific province from Antarctica.

The fossil record of the pectinid *Chlamys* (*sensu lato*) in Antarctica can be traced from the late Eocene La Meseta Formation of Seymour Island (Stilwell & Zinsmeister 1992) to the latest Oligocene Polonez Cove Formation of King George Island (Birkenmajer 1987) and subsurface early Miocene glaciomarine sediments in the McMurdo Sound region (Dell & Fleming 1975). It next appears, in the form of *Chlamys* (*Zygochlamys*) *tuftsensis*, in diatomaceous sediments at Marine Plain, Vestfold Hills and in the Pecten Gravels of Wright Valley, Victoria Land (Turner 1967; Pickard *et al.* 1988). Both these deposits represent the product of substantial marine incursions and can almost certainly be linked to the major early Pliocene warm phase (4.8–3.6 Ma). Probable late Pliocene representatives of the extensive *Chlamys patagonica* species group are also known from Wright Valley, as well as Cockburn Island and Heard Island (Beu 1985). However, at the present day the group is confined to localities in Patagonia and southernmost New Zealand, both of which lie to the north of the Antarctic Convergence. Further late Pliocene and Pleistocene localities are known from both the North Island of New Zealand and southern Tasmania, and it is evident that the range of this group, too, has fluctuated widely in concert with glacial–interglacial cycles (Beu 1985).

Cooling events, as well as being a time when warmer water taxa moved away from Antarctica, may also have facilitated the expansion northwards of cool stenothermal taxa which originated in the highest southern latitudes around Antarctica. For example, it is likely that a range of brachiopods, bivalves, gastropods, asteroids, crinoids, barnacles and decapod crustaceans all had their first occurrence in the late Eocene La Meseta Formation of Seymour Island (Zinsmeister & Feldmann 1984; Wiedman *et al.* 1986; Feldmann & Tshudy 1989). It is believed that taxa such as these evolved in the West Antarctic region and were gradually exported to lower latitudes during phases of global cooling. Biogeographical studies of certain living marine invertebrates, such as imphimediid amphipods and serolid and arcturid isopods, also suggest strongly that they may have originated in the Southern Ocean and dispersed subsequently into lower latitude regions through the later Cenozoic (Watling & Thurston 1989; Brandt 1991).

(*b*) *Vicariant events*

The phenomenon of bipolarity can now be traced back to at least the early Jurassic period (i.e. 200 Ma), and perhaps even further. Although it is not yet possible to determine the precise causes of each of the main phases of bipolar distribution, it is thought that vicariant events may have been consistently important.

Living Antarctic and subantarctic molluscs with bipolar distributions can be grouped into some 14 gastropod and 4 bivalve families (Crame 1993). There are some indications from the fossil record of representatives of four of the commonest families, the buccinids (whelks), naticids, turrids and littorinids, that they underwent a marked diversification through the Miocene epoch. Direct ancestors of all three of these groups can, however, be traced back to the Paleogene, and it is these which may have achieved widespread distribution during the prolonged early middle Eocene – early Miocene cool phase. Vicariance then occurred during early – early middle Miocene global warming, with cool–temperate forms being expelled from the tropics. The late Paleogene – early Neogene may well have been a time when bipolar patterns were formed in many different marine groups (White 1986; Crame 1993). However, this was a period when profound changes occurred in world oceanographic systems; the strengthening of oceanic gyres and steepening of latitudinal temperature gradients may also have enhanced dispersal mechanisms. The role of late Miocene and early Pliocene global warmings in the promotion of climatic vicariance is not yet known.

(*c*) ***Synopsis***

The biogeographic implications of global climate change have yet to be assessed fully. Nevertheless, as the nature and scale of Cenozoic changes become progressively clearer, it is apparent that their effect on biotic distributions on a global scale may have been profound.

A simple intuitive model demonstrates how both a warm-stenothermal and a cool-stenothermal taxon may have responded over a single full climatic cycle. During a warming cycle, warm-stenothermal taxa will expand their latitudinal range, and cold-stenothermal taxa contract; during a cooling cycle the opposite will occur. There is, perhaps, nothing very startling about these patterns as they stand until it is recalled that in the last 2.4 Ma alone there may have been as many as 50 such cycles. Repeated range expansions and contractions of warm-temperate–tropical species may well have stimulated speciation by disruption of distributions into allopatric fragments, followed by renewed contact during the next phase of the cycle. This is likely to have concentrated taxa in equatorial regions, but the same process could also have been going on at the poles. Here, then, is a possible partial explanation of why marine benthic diversity may be high in both equatorial and polar regions; diversity pumps may well function in more than one latitudinal zone (Valentine 1967; Vermeij 1978; Ricklefs 1987). This process may have been going on, intermittently, for more than 200 Ma.

A further key parameter affecting the distribution of benthic marine organisms will be global sea-level change (figure 1). Although magnitude of some of the falls depicted in the curve is still debated, their frequency is not. Over at least the last 30 Ma, sea-level changes have generally (but not always) responded in concert to global marine temperature changes, and the degree of exposure of continental shelves must have at times exerted a considerable influence upon benthic migration patterns. The major discrepancy is probably the correlation of the fall in temperature at the Eocene–Oligocene boundary (36 Ma) with a sea-level rise (figure 1). However it is likely that this is an example of a time-lapse effect related to the growth of the East Antarctic ice cap, since from 35–30 Ma there was a fall in sea level of almost 200 m.

5. AN ASSESSMENT OF FAUNAL RESPONSE TO CENOZOIC CLIMATE CHANGE

Although there is currently much concern over the possible effects of climate change in influencing the evolution of marine faunas, climate is only one of many factors to consider. In the case of the Southern Ocean marine fauna we also need to take into account glaciation, changes in ocean currents, shifts in continental position and palaeolatitude, and sea-level change. A particular difficulty in considering the influence of climate change is that of timescale. In the Southern Ocean we have to consider the following.

1. The long-term change (essentially an overall decline) in Southern Ocean seawater temperature throughout much of the Cenozoic (figure 1).
2. Shorter-term interruptions or fluctuations superimposed on the overall cooling trend, for example, the rise of up to 4°C during the mid-Miocene and the short-term rise of 5–7°C at the Paleocene–Eocene boundary (figure 1; table 1).
3. Short-term cycles and rapid changes. These include Milankovitch cycles and other cycles of much shorter duration. There is also some evidence from both sediment cores (Kennett & Stott 1991) and ice cores Lorius *et al.* 1990) that periods of more or less steady temperature change may be interrupted by sudden and rapid changes of temperature, perhaps as much as 5°C in a few tens of years.
4. Very short-term events. These may leave no trace in the palaeotemperature record but can have severe effects. A good example is the El Niño Southern Oscillation (ENSO) (Arntz & Fahrbach 1991).

Clearly these different processes will produce different effects. Thus the overall cooling between the early Cenozoic and the present day will have driven the evolution of appropriate cooler water physiologies and ecologies (Clarke & Crame 1989; Clarke 1990). Shorter-term fluctuations may have resulted in shifts in geographic distribution and perhaps stimulated periods of taxonomic diversification, whereas very short term or sudden events may have resulted in either local or widespread extinction.

(*a*) ***Temperature adaptation in the modern fauna***

The history of Cenozoic marine temperatures suggests clearly that the marine invertebrates and fish that are found today in the Southern Ocean must have evolved from warmer-water ancestors to live at polar temperatures. As the temperature of their environment cooled, their physiology must have evolved to cope with the change.

The richness and diversity of marine life in the Southern Ocean suggests that modifying physiology to remain viable at sub-zero temperatures has not posed an insuperable evolutionary problem. However, our picture of precisely what adjustments have been needed to allow marine organisms to live in polar waters is still very incomplete. Recent reviews of temperature adaptation in polar marine organisms are given by Johnston (1990) and Clarke (1991).

(*b*) ***Ecological adaptations in the modern fauna***

It is now clear that some important features of the biology of the Southern Ocean marine fauna relate as much to the intense seasonality of the polar marine system as they do to the low temperature. A good example of this is growth rate. The synthesis of new tissue is a physiological process that would be expected to have evolved compensation for temperature. However, most polar marine ectotherms grow more slowly than related warmer-water counterparts, suggesting that the processes involved in growth have been able to evolve very little compensation for temperature. This would make a somewhat paradoxical contrast to those processes which evidently have evolved effective compensation (Clarke 1983, 1991). Part of the explanation for this dichotomy lies in the highly seasonal nature of the food supply for many polar marine organisms which leads to a restricted period for growth within the year, and hence a slow annual growth rate.

Other features which are linked to the seasonality of the polar marine environment include the large overwintering lipid stores of many zooplankton (Clarke & Peck 1991) and the tendency for eggs of polar marine invertebrates to be large (Clarke 1979; Clarke *et al.* 1991). In interpreting fossil evidence it is essential, although not always easy, to distinguish between responses to temperature and responses to ecological factors. Thus the switch from free-spawning to brooding reproductive modes described in fossil echinoids from the Australian Eocene by Foster (1974) is likely to be a response to increased seasonality of food as much as to a decreased temperature.

(*c*) ***The Southern Ocean fauna and climate change***

The diversity of the modern fauna suggests that the long-term cooling since the early Cenozoic has presented no major evolutionary problem. Slow, long-term change would thus appear to be something with which faunas can cope. Indeed it is likely that the marine environment has, in geological terms, never been stable, and organisms have always been tracking those changes, either by adaptive changes to effect temperature compensation or changes in distribution (and very probably both).

Further glaciological and geophysical evidence is required before we can decide whether the continental shelves around Antarctica were ever all covered simultaneously by ice, thus eliminating shallow-water marine habitats. If this ever were the case during the recent glaciation, then the shelves would likely have been recolonized by organisms from deeper water or shallow waters further north. It has long been recognized that several groups may well have moved onto the Antarctic continental shelves from deeper water (and vice versa), and recent detailed analyses have confirmed this for both amphipods and isopods (Watling & Thurston 1989; Brandt 1991). It appears more likely, however, that the extension of continental ice shelves never simultaneously covered all of the shelf and that most (but not necessarily all) taxa were able to survive in unglaciated refugia.

It is nevertheless possible that severe reduction of available shelf areas by extensions of continental ice may explain the loss of some groups. In a recent model of the development of a continental margin under the prolonged influence of a major ice sheet, Hambrey *et al.* (1991) have shown that in the Prydz Bay region of East Antarctica, grounding of the ice sheet at the shelf break occurred in at least the early Oligocene. Subsequently the outer shelf region was subject to a complex sequence of glacial advance and retreat, whereas the inner shelf was the site of erosion of deep coastal channels (see also Larter & Barker 1991). Shallow coastal habitats around Antarctica may thus have been decimated over the last 36 Ma. An important result of these processes may be that the loss of previously important or dominant groups was followed by shifts in the balance of various taxa.

One final point is that the loss of decapods and most groups of bony fish, together with the present success of isopods, amphipods and notothenioid fish, may simply represent the effects of historical contingency (Gould 1989). There may be nothing inherently inferior about those groups that failed, or anything inherently superior about those that diversified into the vacant ecological niches. A replay of the major events of the Cenozoic might lead to a very different fauna from the one we see today around Antarctica.

6. HOW WILL THE FAUNA BE AFFECTED BY FUTURE CLIMATE CHANGE

Predictions of the future are notoriously unreliable. Nevertheless, certain features of the present fauna allow us to make a number of informed guesses as to how it might respond to continued climate change, although these are necessarily surrounded by caveats.

The present thermal régime in the Southern Ocean is (on the scale of the lifespan of a typical marine organism) very stable, particularly close to the Antarctic continent (Clarke 1983), and this is probably associated with a high level of stenothermy in the fauna. Taken together these factors would suggest that any warming of the seas around Antarctica might have severe consequences on the fauna (Berkman 1991). This is because the present fauna has been selected for a physiology that is tuned to a narrow range of temperatures, and the example of the fate of some tropical organisms in the Pliocene cooling phase (Stanley 1984) suggests that this may limit ability to adapt to changing temperatures. Furthermore, the continental shelves around Antarctica are isolated from other areas of shallow sea by large tracts of deep water. Because many species reproduce via short-lived lecithotrophic larvae or brooded eggs leading to miniature adults rather than larvae (Dell 1972), opportunities for dispersal are reduced.

It might be expected that a general warming of the Southern Ocean would allow more temperate species to invade from lower latitudes. A number of factors, however, may mean that this exchange is slower than it might otherwise be. Firstly, many cool-temperate species have reproductive strategies that would appear to limit dispersal ability (low fecundity because of larger eggs, direct development or brooding, reduced pelagic larval stages). Secondly, it is clear from present distribution patterns that the Polar Frontal Zone acts as a strong (but not necessarily absolute) barrier to dispersal in or out of the Southern Ocean for many taxa.

Although this may seem an obvious conclusion, and one that suggests that adaptation to the cold but seasonal Southern Ocean may have taken the fauna up an evolutionary cul-de-sac, geological history suggests this may not be so. Faunas in the past have been able to cope with global warming, and it may even be that environmental change is a stimulus to evolution. In the long-term view, perhaps global change, at least on the scale so far experienced by the marine realm, is no bad thing after all.

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Discussion

J.-O. Strömberg (*Kristine bergs Marinbiologiska Station, Fiskebäckskil, Sweden*). There is one factor related to animal distribution and dispersal that Professor Clarke did not mention, and that is that the Antarctic continent is surrounded by a deep sea. This might have a fundamental importance in this context; for example, the missing decapods in Antarctica. Decapods do not thrive in the deep sea. This might be part of an explanation why decapods have not managed to colonize Antarctic shelves after they once went extinct there. Is this conceivable?

A. Clarke. I am sure Professor Strömberg is correct that the deep-sea environment surrounding Antarctica has had great importance for the history of the Southern Ocean marine fauna. It is clear that there are close taxonomic connections between the shelf fauna and the deep sea for some groups in Antarctica (for example isopods), but whether an inability to adapt to the deep sea during a glacial maximum might explain the low numbers of decapods in Antarctica is not clear. Simple ecological observations rarely have simple explanations and my personal suspicion is that the paucity of Southern Ocean decapods may be the result of a whole suite of selective pressures.

P. F. Barker (*British Antarctic Survey, Cambridge, U.K.*). Professor Clarke mentioned an apparent disagreement between the conclusion that ice sheets were grounded to the continental shelf edge all around Antarctica during glacial maxima, and the richness of the benthic community on the Antarctic shelf at present. All evidence from the continental shelf to date is consistent with the shelf-edge grounding model: is it plausible that the benthic community should have been able to survive during glacial maxima on the uppermost continental slope (except in areas of most rapid sedimentation), to re-colonize the shelf once the ice sheet grounding line had again retreated?

A. Clarke. I believe Dr Barker has highlighted a crucial question. Clearly at periods of glacial maxima in the past the continental ice shelves would have been greater than at present, and would have extended over the continental shelves further than they do at present. At such times the fauna would have had to retreat to refugia, and there is some evidence (for example from amphipods and isopods) that a retreat to the uppermost continental slope may well have been important. However, the biological evidence we have at present would suggest that there were sufficient refugia to maintain a rich and diverse fauna even through periods of glacial maxima.